

A laboratory study of agonistic behaviour in the Red musk shrew, *Crocidura flavescens* (I. Geoffroy, 1827)

By R. M. BAXTER and D. IRWIN

Department of Zoology, University of Natal, Pietermaritzburg, South Africa

*Receipt of Ms. 30. 07. 1992
Acceptance of Ms. 09. 06. 1995*

Abstract

Investigated the agonistic behaviour in male and female *Crocidura flavescens* under conditions of increasing confinement in the laboratory. Nine sexually mature shrews (four male and five female) were used and six paired encounters were run for each sex. Initially each pair was confined to 1800 cm² but this was reduced to 900 cm² and finally 450 cm² before the encounter was ended. No encounter lasted more than 12 minutes and all audible and visible behaviour was recorded. Two encounters were filmed for analysis.

Seven postures and 16 other non-fighting behaviours can be distinguished and the frequency of eight of these differs significantly between the sexes. These components of agonistic behaviour may have preparatory, sensory, communicative and regenerative value and a hierarchy, which would preclude fighting under natural conditions, may exist.

Males are significantly more aggressive than females both in the frequency and latency of fighting. Increasing spatial confinement significantly increases the frequency of fighting in both males and females.

C. flavescens is considered to be asocial with males indicating a greater tendency for territorial behaviour through being more aggressive and scent marking more frequently than females.

Introduction

In general, studies on the agonistic behaviour and social organization of shrews have been restricted to European and North American species in captivity; inter alia *Sorex araneus* (CROWCROFT 1957), *Blarina brevicauda* (OLSEN 1969), *Crocidura russula* (VOGEL 1969), *Neomys fodiens* (MICHALAK 1983) while GOULDEN and MEESTER (1978) and BAXTER and MEESTER (1980, 1982) have provided some qualitative data on some southern African species. Field studies on social organization and territoriality in inter alia *B. brevicauda* (PLATT 1976) and *C. russula* (CANTONI and VOGEL 1989) as well as inter- and intraspecific competition in *S. araneus* and *S. minutus* (CROIN MICHIELSEN 1966) provide valuable data.

As yet, no detailed quantitative research on agonistic behaviour has been conducted on an African soricid. Consequently, this study was undertaken to describe, analyse and determine the possible functions of the components of agonistic behaviour in *Crocidura flavescens* as well as determine whether differences exist between males and females in this regard.

C. flavescens is a large shrew with a mean total length of 149.1 mm (MEESTER 1963) and usually a mass of between 20 and 30 g. There is significant sexual dimorphism (MEESTER 1963) with a mean mass difference of 4.5 g in favour of males (RAUTENBACH 1978).

Material and methods

The shrews were trapped during winter in Scottsville, Pietermaritzburg using PVC livetraps (WILLAN 1979) baited with minced oxheart. Prior to experimentation all shrews had attained sexual maturity. Exact ages were not determined but all would have been born during the preceding summer because older adults do not appear to survive the onset of a second winter (BAXTER 1977).

Captive shrews were kept singly in glass aquaria ($60 \times 30 \times 30$ cm) under semi-controlled conditions at $20\text{--}25^\circ\text{C}$ with a 14 h:10 h light:dark regime. The minimum period in captivity prior to experimentation was four weeks. During this period the animals were sexed and marked in order to allow easy individual recognition.

All trials were carried out in a neutral, territorially unproclaimed glass aquarium (floor area = 1800 cm^2) which had 5 cm of soil in the bottom. After each trial, the area was swept thoroughly to disperse odour left by scent marking, all faeces were removed and the inner surface of the glass was cleaned with a wet cloth. The trial area could be partitioned into two separate areas of variable size by inserting a sheet of hardboard. All trials were run indoors between 10.00 h and 18.00 h when the activity profile of captive *C. flavescens* approximates to its mean daytime value in captivity of 13% (BAXTER et al. 1979). Light was provided by fluorescent tubes and daylight, and temperature ranged from $18\text{--}25^\circ\text{C}$. Noise and disturbances were kept to a minimum. No two shrews encountered one another more than once and then always one of the same sex.

The male sample ($n = 4$) allowed six paired combinations without repetition and although there were five females, only six trials were run so that the resultant data were more readily comparable. All trials involving a specific individual were run at least 24 hours apart in order to prevent fatigue. Trials were run by partitioning the trial area, releasing a shrew into each half and allowing them to settle down for about a minute. The pairs were subjected to three conditions of increasing spatial confinement; 1800 cm^2 , 900 cm^2 and 450 cm^2 . This meant that one of the shrews was progressively forced into the area occupied by the other. This method would have biased the results if winners/losers were being determined but as this was not the case, potential bias was nullified.

Initially the partition was removed for 5–6 minutes, resulting in the two shrews being jointly enclosed in a total area = 1800 cm^2 . Thereafter they were again separated for 30 s. The shrews were then confined in one half of the trial area (900 cm^2) for 2.5–3 minutes, briefly separated again, before being confined in one quarter of the area (450 cm^2) for 2.5–3 minutes. The shrews were then returned to their "home" aquaria.

The full duration of each trial was timed and all visible and audible behaviour was recorded by dictation into a cassette tape recorder. This provided data regarding the nature, frequency and duration of observed behaviours. Two encounters, one between males and another between females, were filmed using a cine camera (Paillard-Bolex H16 Reflex) with lighting provided by a 500 watt incandescent bulb supported 120 cm above the trial area.

Results

Statistical analysis

The total time spent under all conditions by males was 62 min 30 s and by females, 76 min 20 s. The total number of fights (directed aggressive physical contact) was recorded under each condition and fighting frequency (fights/min) for both sexes was calculated for these conditions (see Tab. 1), and then subjected to a Friedman two-way analysis of variance (SIEGEL 1956).

The effect of confinement in increasing fighting frequency was found to be highly significant in both sexes (M, $p = 0.0046$; F, $p = 0.0007$). Neither males ($p = 0.446$) nor females ($p = 0.5$) differed significantly among themselves. Mean fighting frequency was calculated for each shrew across all three conditions (Tab. 1) and males showed an overall mean significantly higher than that of females ($p = 0.016$).

The mean latency of fighting under condition 1 (1800 cm^2), being the time from removal of the partition to the first fight or in the case of some females the period in which no fighting occurred, was 60 seconds in males and 4 min 28 s in females (three females did not fight). Males came into conflict significantly sooner than females ($p = 0.013$) indicating a higher level of agonistic activity.

Table 1. Mean frequencies of fighting for each individual shrew under each experimental condition. The means were obtained from three trials for each male and three or less for each female.

Male <i>C. flavescens</i>					Female <i>C. flavescens</i>				
Area/ shrew	1 800 cm ²	900 cm ²	450 cm ²	\bar{x} (M)	Area/ shrew	1 800 cm ²	900 cm ²	450 cm ²	\bar{x} (F)
M1	1.66	4.58	7.79	3.13	F1	0.17	1.29	6.80	0.92
M2	2.22	2.30	13.00	3.37	F2	0.22	1.78	6.97	0.98
M3	1.12	3.22	5.65	2.06	F3	0.00	1.24	5.65	1.52
M4	1.57	4.77	12.00	3.50	F4	1.04	3.16	6.40	2.50
					F5	0.80	1.60	5.23	1.73
\bar{x} /area	1.64	3.71	9.61		\bar{x} /area	0.45	1.81	6.21	
	Overall mean (M)			3.01		Overall mean (M)			1.52
	S.D.			0.654		S.D.			0.635

Postures

Seven postures were distinguished in *C. flavescens* and the differences between the sexes in their frequency of occurrence, as well as those of a variety of other behaviours associated with agonism, are summarized in table 2.

Hunched: This is a squat posture with the head lowered and back slightly arched. Unlike freezing it often involves walking or, when seen in resting shrews, is associated with grooming, scratching and orientation reactions (Fig. 1 A).

Raised I: This is a quadrupedal stance similar to Hunched but with the head raised in orientation to sensory stimuli (Fig. 1 B).

Raised II: This is an extension of Raised I with the forequarters raised 1–2 cm above the substrate by extending the forelimbs (Fig. 1 C). This posture was noted in *Crociodura flavescens herero* (= *C. occidentalis* MEESTER et al. 1986) by MARLOW (1955). Raised I and II are referred to collectively as “stance” by OLSEN (1969) and PLATT (1976), and are often accompanied by vocalization and bared teeth. They may precede either avoidance or attack.

Hunched and Raised I and II are more common in females.

Tripedal: This is an important preparatory posture characterized by raising the fore-foot nearest the opponent shrew (Fig. 1 D). Tripedal posture is known in several soricids (OLSEN 1969; PLATT 1976). It may precede or follow a number of other behaviours. It is regarded as aggressive by PLATT (1976) and is more common in *C. flavescens* males.

Sideways: This is a side-on orientation of the body to the opponent (tripedal or quadrupedal) and is usually defensive. This posture may lead to the shrew rolling over with the fore- and hind limb on one side raised, exposing the belly, and ultimately to “Tantrum”. In *C. flavescens* the sideways posture was always very brief and was significantly more common in males ($p = 0.032$). PLATT (1976) considers this to be a submissive posture.

Rearing: This is equivalent to the ‘upright’ posture described by OLSEN (1969), involving raising the body to a vertical position on the hind limbs, exposing the ventrum. This posture is well known in intraspecific conflicts in shrews (CROWCROFT 1957; EISENBERG 1964; OLSEN 1969; BAXTER and MEESTER 1982). It is usually accompanied by vocalization

Table 2. Summary of observed agonistic behaviours in *Crocidura flavescens* showing the observed frequency of occurrence of the behaviours as well as the frequencies per unit time. The probabilities reported were obtained by testing for differences between the frequencies per unit time for males and females. An asterisk indicates significance at the 95% level and the final column indicates in which sex the behaviour is most common.

Behaviour	Duration of M encounters 62 min 30 s			Duration of F encounters 76 min 20 s			Most com- in ... M/F
	Frequency of Occurrence	Frequency per Unit Time	Frequency of Occurrence	Frequency per Unit Time	Probability		
Postures	Hunched	5	8.0	12	15.7	0.119	F
	Raised I	2	3.2	3	3.9	0.206	F
	Raised II	13	20.8	17	22.2	0.278	F
	Tripedal	21	33.6	6	7.8	0.278	M
	Sideways	7	11.2	2	2.6	0.032*	M
	Rearing	6	9.6	3	3.9	0.206	M
	Tantrum	17	27.2	5	6.5	0.095	M
	Baring teeth	9	14.4	10	13.0	0.548	
Passive avoidance	Freezing	7	11.2	29	37.9	0.016*	F
Active avoidance	Running	11	17.6	8	10.4	0.321	M
	Jumping	19	30.4	6	7.8	0.024*	M
	Escape	15	24.0	22	28.8	0.206	F
Approach		25	40.0	24	31.4	0.365	M
Attack	Chasing and biting	43	68.8	13	17.0	0.016*	M
	Jumping	9	14.4	3	3.9	0.056	M
	Hopping	16	25.6	3	3.9	0.024*	M
Fighting		187	299.0	103	134.8	0.016*	M
Other activities	Grooming	26	41.6	31	40.5	0.365	F
	Scratching	3	4.8	4	5.2	0.365	F
	Digging	20	32.0	9	11.7	0.056	M
	Redirected attack	4	6.4	0	0	0.001*	M
Scent marking	Flank	2	3.2	0	0	0.001*	M
	Chin	24	38.4	6	7.8	0.032*	M
	Anal	4	6.4	3	3.9	0.452	M

and 'boxing' with the forepaws (Fig. 2 A). However, when observed under neutral conditions in *C. flavescens* Rearing was transient, usually leading immediately to either avoidance or "Tantrum" postures. It was observed twice in an inoffensive situation when a shrew reared up to scent the air with the tail providing extra support. Rearing is more common in males and is probably submissive.

"Tantrum": This was called 'back' by OLSEN (1969) and may be described as a period (1-8 s) of vocalization and kicking while the shrew lies on its back, with the head slightly

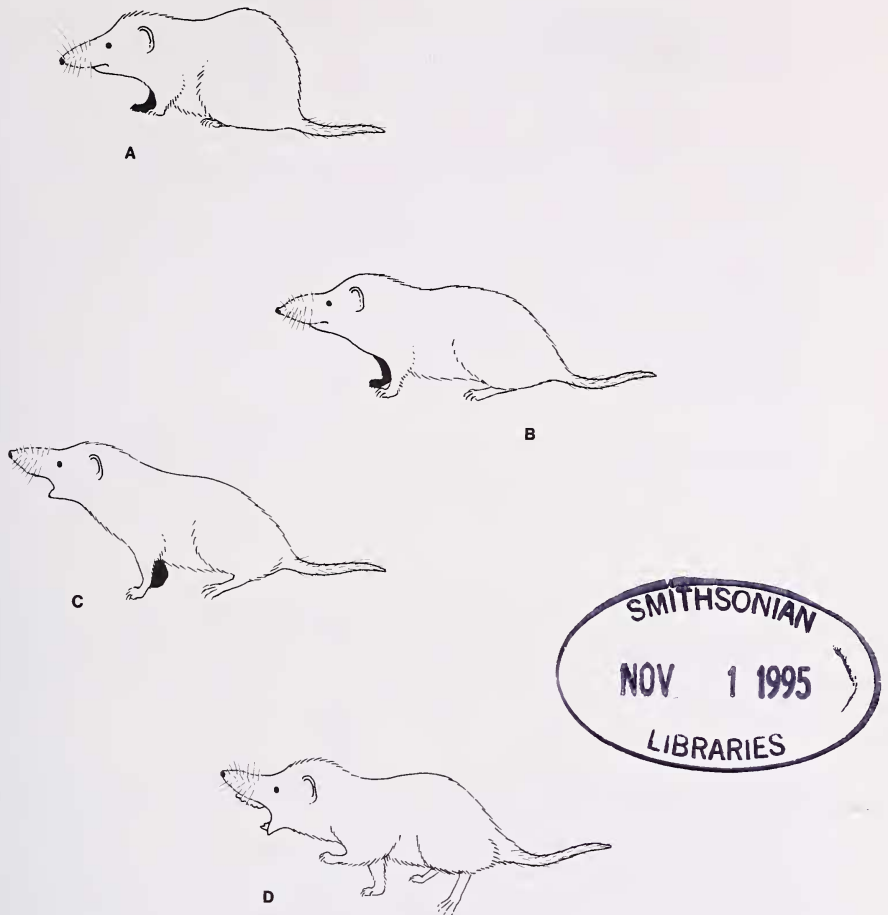


Fig. 1. Some postures seen during agonistic encounters; A. Hunched; B. Raised I; C. Raised II; D. Tripedal with teeth bared.

raised. It is considered submissive here, as in PLATT (1976), but BUNN (1966) considers it dominant.

"Tantrum" did not always result in cessation of attack. Frequently both shrews performed this behaviour simultaneously after a fight. "Tantrum" always followed either Sideways or Rearing postures. It was more common in males ($p = 0.095$) (Fig. 2 B).

No characteristic tail postures were noted in *C. flavescens*. EISENBERG (1964) and OLSEN (1969) have noted such postures in *Sorex* and *Blarina* sp. and HANSELL and AITKEN (1977) refer to tail-lashing in *Sorex*. Stamping of the forefeet (PLATT 1976) was not seen in *C. flavescens*.

Baring of the teeth with the lips drawn back to reveal the upper premolars was noted in all postures except Hunched. Exposure of the teeth while vocalizing was not regarded as 'baring teeth', hence the low recorded frequency of this activity in table 2.

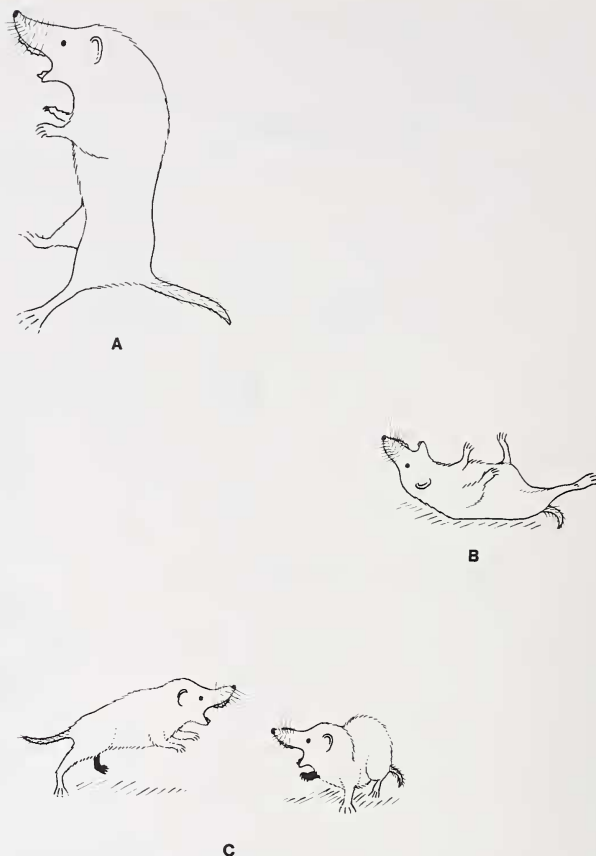


Fig. 2. Additional postures seen during agonistic encounters: A. Rearing; B. "Tantrum"; C. A hopping attack against a tripedal, sideways *C. flavescens*.

Vocalization

This occurred in all individuals and had communicative value. The short high-pitched squeak which is characteristic of agonistic behaviour, is known in many sorcids (see inter alia GOULD 1969; BAXTER and MEESTER 1982; CHURCHFIELD 1990). In *C. flavescens* it showed frequencies of 10–50 kHz, and was emitted singly or in sporadic bursts and associated with all activities except the Hunched posture, freezing, grooming, scratching and scent marking.

PLATT (1976) reported vocalization in nine out of ten tripedal and all quadrupedal 'stances'.

Avoidance

Passive avoidance (freezing) resulted in the entire shrew, except the vibrissae and snout, being immobile. Freezing was seen to occur in Hunched, Raised I and II and Tripedal postures; it was significantly more common in females ($p = 0.016$). Active avoidance involved running and jumping. Mutual avoidance, however, was overall the most common behav-

our pattern noted, but decreased in frequency under more confined conditions. It occurred most often on accidental physical contact, whereupon both shrews would leap apart and possibly vocalize, as has been reported by CROWCROFT (1957), EISENBERG (1964), BAXTER and MEESTER (1980, 1982).

Running was generally thigmotaxic and often led to the shrews encountering one another yet again whereupon fighting occurred. It was more common in males, as was avoidance by jumping over or away from the opponent shrew ($p = 0.024$). OLSEN (1969) reported jumping as a means of avoidance in *B. brevicauda*. Avoidance was sometimes preceded by Raised, Tripedal, Sideways or Rearing postures in *C. flavescens*.

It appears then that males, being more active under the experimental conditions, attempted to avoid one another by actively running or jumping. More activity resulted in frequent contact, reflected in the high frequency and low latency of fighting. In contrast, females moved about less than males, avoiding one another passively by freezing and hunching at opposite ends of the trial area. The result was fewer physical contacts, shown by their low frequency and high latency of fighting.

All individuals unsuccessfully attempted to escape from the trial aquarium by jumping or by digging under the partition when it was in place. This behaviour was more common in females.

Approach

This was defined as locomotion directed towards the opponent shrew regardless of the orientation of the shrews relative to one another. It occurred with similar frequency in males and females and included running and walking but not hopping or jumping.

Attack

This involved directed antagonistic behaviour such as biting and chasing and was sometimes mutually undertaken. OLSEN (1969) considered chasing rare on neutral ground while EISENBERG (1964) found that almost all chasing, fighting and flight occurred during interaction between strange shrews. In *C. flavescens* attack was significantly more frequent in males ($p = 0.016$).

In hopping attacks (Fig. 2C) the forefeet were lifted clear of the ground as the shrew moved towards its opponent in jerky hops of 0.5–1.5 cm. Hopping attacks were significantly more common in males ($p = 0.024$).

In jumping attacks the aggressor jumped onto its opponent from a distance of 5–15 cm. Again, this was significantly more common in males ($p = 0.056$).

Other activities

These were evident during the agonistic behaviour of *C. flavescens*. Grooming consisted of rubbing the muzzle, and nibbling and licking the forepaws. Scratching of the body was done with either hind foot. They were performed in the Hunched posture only, consequently occurring more frequently in females.

Digging was more common in males ($p = 0.056$) and usually occurred after fighting. It could be distinguished from escape attempts as it was performed aimlessly, was never prolonged, and was frequently accompanied by vocalization. The hind feet were often employed to some extent, unlike directed digging where only the forefeet were used.

Redirected attack on the sides of the trial aquarium, or on what appeared to be an invisible opponent, occurred only in males and was rare, usually beginning as a jump and leading to digging, running, or further jumping. It most probably indicates a higher level of agonistic arousal.

Scent marking

This can be performed in three different ways (BAXTER and MEESTER 1982). Flank marking using the lateral glands was seen only in males. Neck marking, the most commonly used method in *C. flavescens* which involves ploughing the chin and neck along the substrate with slight side to side movements, was significantly more frequent in males ($p = 0.032$). DRYDEN and CONAWAY (1967) regard the neck glands as the most important area for scent production. Anal marking is described as 'ventral rub' by PLATT (1976) who found it more common in males of *B. brevicauda*. It involved dragging the ventral surface (especially the anogenital region) along the substrate, often with a concave shaping of the back. It was performed with approximately equal frequency by both sexes although BAXTER and MEESTER (1982) noted it only after fighting in males.

As scent is used for territorial demarcation in shrews (PLATT 1976) the frequency of scent marking may be regarded as an index of territoriality. Neutral ground may be rapidly proclaimed as territory. This was suggested by the frequent return of each shrew to the end of the trial area into which it was first released, before commencement of regenerative behaviour or scent marking. The higher frequency of scent marking in males suggests that they are territorial, which would coincide with their aggressiveness and low tolerance of conspecifics.

Perception

There are no quantitative data on the acuity of the various senses in soricids. Vision appears to be poorly developed, as no evidence of visual communication has been found (GOULD 1969; CHURCHFIELD 1990). A mirror placed in the trial aquarium with a single male *C. flavescens* elicited no agonistic behavioural response.

Olfaction appears to play an important role in agonistic behaviour, as suggested by the frequency of scent marking and by smelling of the air and surroundings by shrews in Hunched, Raised I & II and Rearing postures.

Tactile cues were used extensively. The mystacial vibrissae were extremely sensitive to stimulation; accidental contacts were frequently avoided by tactile sense when the two shrews appeared to be unaware of one another's positions in the trial area.

Hearing is acute in shrews (GOULD 1969; GRÜNWARD 1969; BAXTER and MEESTER 1982), but unlike some other soricids (GOULD et al. 1964; BUCHLER 1976; TOMASI 1979), *C. flavescens* does not echolocate (IRWIN and BAXTER 1980).

Directed vocalization by an opponent in a Raised II or Tripedal posture often resulted in an instantaneous orientation reaction (Raised I, II or Tripedal postures) or fear reaction (passive or active avoidance) in the perceiving shrew. Similar reactions occurred in response to digging, movement of the partition, and voices.

The relationship between the observed behaviours are summarized in figure 3.

Discussion

The functional value of the postures and associated agonistic behaviours may be assessed from the point of view of the animals performing them, to which the outcome is of primary importance. Four functions are proposed; preparatory, sensory, communicative and regenerative.

Preparatory: All these behaviours begin either tri- or quadrupedally and the include Raised I and II, Tripedal, Sideways and Rearing postures, and baring the teeth. Each of these prepares the animal for either fighting or avoidance.

Sensory; Freezing, Hunched, Raised I and II, Tripedal and to a lesser extent Sideways and Rearing postures are involved in sensory orientation. Hunching is a lower-order sensory posture, which through stimulation gives rise to higher-order postures such as Raised II and Tripedal. Sideways has limited sensory function while freezing is a higher-order sensory (and passive protective) behaviour, always accompanied by olfaction.

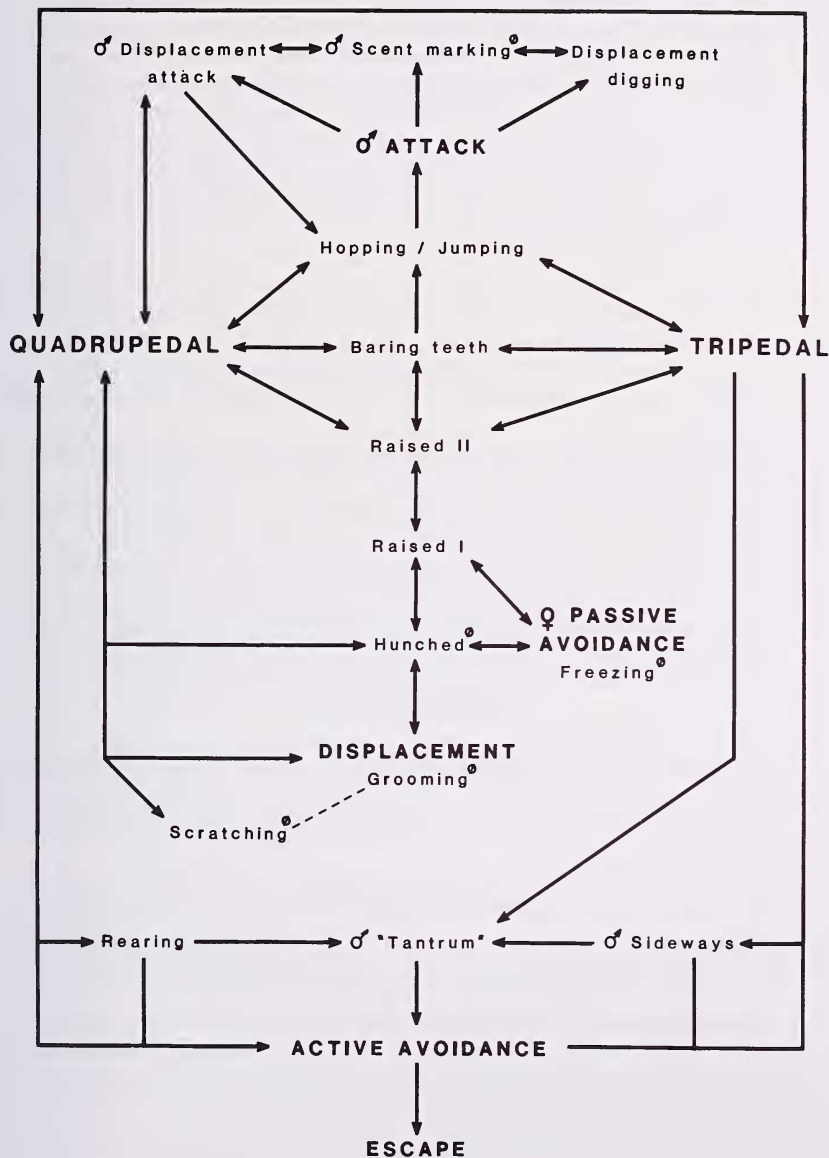


Fig. 3. The progression of and relationship between the observed agonistic behaviours. The presence of ♂ or ♀ signs at a particular behaviour indicates that it is significantly more common in that particular sex. (∅ indicates absence of vocalization.)

Communicative: Probably the most important function of posturing is communication. It is doubtful whether postures have any visual communicative value (GOULD 1969), considering the poor vision of soricids.

OLSEN (1969) considered the five postures of *B. brevicauda* to have 'threat' and possibly species-recognition function, as they served to intimidate conspecific opponents.

The signal value of Raised I and II, Tripedal, Sideways, Rearing and "Tantrum" postures is mainly the accompanying vocalization, which has high communicative value. All of the above also expose scent-producing areas on the body. The most important area, the neck (DRYDEN and CONAWAY 1967), is exposed Raised I and II, Tripedal and Rearing while lateral glands are exposed in Sideways and Rearing and anogenital glands in Rearing and "Tantrum" postures. BAXTER and MEESTER (1982) suggest that exposing the neck in the raised posture acts aggressively by transmitting individual odour to the opponent.

OLSEN (1969) suggests that scent may also be related to the species-recognition function in reducing conspecific predation. Cannibalism is, however, known in captive shrews (BAXTER and MEESTER 1982) and attack on the ventral surface is not always inhibited by submissive and scent-emitting postures.

Regenerative; Sporadic interludes in fighting occurred by 'mutual consent' in all trials, and were characterized by hunching postures to groom and lick wounds. It is doubtful whether such a stage would be reached in agonistic behaviour under natural conditions where avoidance may be more permanent.

A hierarchy of behaviours may be suggested for agonistic interactions in *C. flavescens*.

1. On neutral ground, vocalization (in Raised I, Raised II or Tripedal posture) and mutual avoidance would occur.
2. Should one shrew persist in aggressive behaviour, as in territorial conflicts, chasing and avoidance would ensue.
3. If long-term avoidance (escape) is not possible in 1 or 2 above, posturing would become more intense.
4. If these mechanisms failed to achieve separation of the two shrews, fighting would ensue.

C. flavescens (and probably most other soricids) would therefore only fight if other separating mechanisms lower in the hierarchy failed. The four levels described in this hierarchy correspond with the four levels of aggression described by BAXTER and MEESTER (1982).

Under natural conditions fighting between shrews is a rare occurrence (CROWCROFT 1957; EISENBERG 1964; OLSEN 1969), with mutual avoidance being the predominant response to contact on neutral ground and chasing and active avoidance the main responses to territorial conflict (CROWCROFT 1957). CHURCHFIELD (1990), however, has observed fighting under natural conditions.

The results of this study indicates that *C. flavescens* males are more aggressive and perform more scent marking than females. The fact that they are both highly aggressive, suggests they both maintain territories but that the females' territories are less rigorously maintained. It is likely that they are asocial as BAXTER (1977) has indicated that when paired in captivity, the individuals show continuing aggression for up to a week, before nesting together. After mating, the female becomes highly aggressive and drives the male from the shared nest. Under natural conditions, BAXTER (1977) suggests that this manifest aggression would preclude any form of social organization other than asocial. The levels of aggression shown in this study tend to support this suggestion. VOGEL (in litt.) has found the level of aggression shown by *C. flavescens* in contradiction with the high population densities he found in Mali, but ROWE-ROWE (pers. comm.) has found distinct territorial boundary between two wild males, thus supporting the suggestions of this study.

VOGEL (1978) states that the Crocidurinae tend to show low territoriality and CANTONI and VOGEL (1989) have shown that *C. russula* have communal nests in winter. They state

further that the offspring are tolerated for several weeks after weaning, a situation very different from that of *C. flavescens*. BAXTER (1977) found that the young of this species have to be removed from their natal cage by Day 28 in order to prevent parent-offspring aggression which can lead to death. This, together with the fact that both male and female *Myosorex varius*, a species sympatric with *C. flavescens*, are relatively social in captivity (eight adults as opposed to two *C. flavescens*, cohabit peacefully in captivity (BAXTER unpubl. data), but maintain territories throughout the year (BAXTER and LLOYD unpubl. data), implies that the present suggestion of asocial territoriality in *C. flavescens* is valid.

Solitary habit and territoriality serve several functions in small predators, the most important of which is the reduction of intraspecific competition for the available food by spacing the population out evenly over the available habitat (CROWCROFT 1957; EISENBERG 1964; CROIN MICHELSEN 1966; OLSEN 1969; PLATT 1976). Rigorous territoriality regardless of sex is found in *S. araneus* and *S. minutus* populations and is considered to have the primary function of conserving a food supply that will last through the winter when prey density is low. This is described as 'single unit' territoriality (one animal of the species per territory, without overlap); such territories alter their size and position in response to factors such as prey density and the energy requirements of the shrew populations (CROIN MICHELSEN 1966).

M. varius does not show single unit territoriality (BAXTER and LLOYD unpubl. data) and one might expect the same in *C. flavescens* as the sub-tropical African climate is not as severe as that of the Northern temperate regions. It is doubtful whether the food supply is affected adversely enough in winter to demand 'single unit' territoriality in southern African soricids.

The territories of males and females may overlap (as has been found in *Myosorex varius* (BAXTER and LLOYD unpubl. data)) if competition for food is not intense. This overlap may increase during summer (when food is more readily available) allowing breeding to occur without the massive breakdown of territorial boundaries noted in *Sorex* (CROIN MICHELSEN 1966).

Obviously further research is needed to investigate the pugnacious *C. flavescens* and the nature of its aggression, preferably using marked animals in a field situation.

Acknowledgements

We would like to thank the University of Natal, Pietermaritzburg for financial assistance. Dr. R. PLUNKETT and Dr. B. FAULDS are thanked for their constructive criticism. AXEL DIEFENBACH is thanked for his assistance with the German summary.

Zusammenfassung

Eine Laboruntersuchung über das agonistische Verhalten der afrikanischen Roten Riesenspitzmaus, Crocidura flavescens (I. Geoffroy, 1827).

Diese Laboruntersuchung befaßt sich mit dem agonistischen Verhalten von männlichen und weiblichen *Crocidura flavescens* unter eingeschränkten Raumverhältnissen. Neun fortpflanzungsfähige Spitzmäuse (vier männliche und fünf weibliche) wurden untersucht indem Auseinandersetzungen in jedem Geschlecht durchgeführt wurden. Anfänglich standen jedem Paar 1800 cm² Fläche zur Verfügung. Der vorhandene Raum wurde noch vor Beendigung der Auseinandersetzung auf 900 cm² und schließlich auf 450 cm² verringert. Keine Auseinandersetzung dauerte länger als 12 Minuten und alle akustischen und sichtbaren Verhaltensweisen wurden aufgenommen. Zwei Auseinandersetzungen wurden gefilmt, um anschließend im Detail untersucht werden zu können.

Sieben körperliche Stellungen und 16 andere nicht kämpferische Verhaltensweisen können unterschieden werden. Von den 16 nicht kämpferischen Verhaltensweisen unterschieden sich acht im Vor-

kommen ihrer Häufigkeit wesentlich zwischen den Geschlechtern. Diese Bestandteile des agonistischen Verhaltens könnten einen vorbereitenden, sensorischen kommunikativen und regenerativen Wert haben, und somit könnten Verhaltensweisen in bestimmter Hierarchie vorliegen, die unter natürlichen Lebensbedingungen kämpferische Auseinandersetzungen nicht aufkommen lassen.

Männchen sind wesentlich angriffslustiger als Weibchen sowohl in der Häufigkeit wie auch der Länge der Auseinandersetzung. Zunehmende räumliche Einengung steigert wesentlich die Häufigkeit der kämpferischen Auseinandersetzung sowohl bei den Männchen als auch bei den Weibchen.

Crocidura flavescens wird als unsozial betrachtet. Männchen zeigen eine größere Tendenz für territoriales Verhalten durch stärkere Aggressivität und häufigeres Duftmarkieren im Vergleich zu Weibchen.

References

- BAXTER, R. M. (1977): The biology of captive *Crocidura flavescens*, with reference to other southern African soricids. University of Natal, Pietermaritzburg: M. Sc. thesis.
- BAXTER, R. M.; MEESTER, J. (1980): Notes on the captive behaviour of five species of southern African shrews. *Säugetierkd. Mitt.* **40**, 55–62.
- (1982): The captive behaviour of the red musk shrew *Crocidura f. flavescens* (I. Geoffroy, 1827) (Soricidae: Crocidurinae). *Mammalia* **46**, 11–27.
- BAXTER, R. M.; GOULDEN, E. A.; MEESTER, J. (1979): The activity patterns of some southern African *Crocidura* in captivity. *Acta theriol.* **24**, 61–68.
- BUCHLER, E. R. (1976): The use of echolocation by the wandering shrew (*Sorex vagrans*). *Anim. Behav.* **24**, 858–873.
- BUNN, D. S. (1966): Fighting and moult in shrews. *J. Zool. (London)* **148**, 580–582.
- CANTONI, D.; VOGEL, P. (1989): Social organization and mating system of free-ranging, greater white-toothed shrews, *Crocidura russula*. *Anim. Behav.* **38**, 205–214.
- CHURCHFIELD, S. (1990): The natural history of shrews. London: Christopher Helm.
- CROIN MICHIELSEN, N. (1966): Intraspecific and interspecific competition in the shrews *Sorex araneus* L. and *S. minutus* L. *Arch. néerl. Zool.* **17**, 73–174.
- CROWCROFT, P. (1957): The life of the shrew. London: Max Rheinhart.
- DRYDEN, G. L.; CONAWAY, C. H. (1967): The origin and hormonal control of scent production in *Suncus murinus*. *J. Mammalogy* **48**, 420–428.
- EISENBERG, J. F. (1964): Studies on the behaviour of *Sorex vagrans*. *Am. Midl. Nat.* **72**, 417–425.
- GOULD, E. (1969): Communication in three genera of shrews (Soricidae): *Suncus*, *Blarina* and *Cryptotis*. *Behav. Sci., Ser. Biol.* **3**, 11–31.
- GOULD, E.; NEGUS, N. C.; NOVICK, A. (1964): Evidence for echolocation in shrews. *J. exp. Zool.* **156**, 19–38.
- GOULDEN, E. A.; MEESTER (1978): Notes on the behaviour of *Crocidura* and *Myosorex* in captivity. *Mammalia* **42**, 197–207.
- GRÜNWARD, A. (1969): Untersuchungen zur Orientierung der Weißzahnschnecken (Soricidae – Crocidurinae). *Z. vergl. Physiol.* **65**, 191–217.
- HANSELL, M. H.; AIKEN, J. J. (1977): Experimental animal behaviour – a selection of laboratory exercises. Glasgow: Blackie.
- IRWIN, D. V.; BAXTER, R. M. (1980): Evidence against the use of echolocation by *Crocidura f. flavescens* (Soricidae). *Säugetierkd. Mitt.* **28**, 323.
- MARLOW, B. J. G. (1955): Observations on the herero musk shrew *Crocidura flavescens herero* St. Leger, in captivity. *Proc. zool. Soc. Lond.* **124**, 803–808.
- MEESTER, J. (1963): A systematic revision of the shrew genus *Crocidura* in southern Africa. *Transv. Mus. Mem.* **13**, 1–127.
- MEESTER, J. A. J.; RAUTENBACH, I. L.; DIPPENAAR, N. J.; BAKER, C. M. (1986): Classification of southern African mammals. *Transv. Mus. Monogr.* **5**, 1–359.
- MICHALAK, I. (1983): Reproduction, maternal and social behaviour of the European water shrew under laboratory conditions. *Acta theriol.* **28**, 1–24.
- OLSEN, R. W. (1969): Agonistic behaviour of the short-tailed shrew (*Blarina brevicauda*). *J. Mammalogy* **50**, 494–500.
- PLATT, W. J. (1976): The social organization and territoriality of short-tailed shrew (*Blarina brevicauda*) populations in old-field habitats. *Anim. Behav.* **24**, 305–318.

- RAUTENBACH, I. L. (1978): The mammals of the Transvaal. University of Natal, Pietermaritzburg: Ph. D thesis.
- SIEGEL, S. (1956): Nonparametric statistics for the behavioural sciences. Tokyo: McGraw-Hill.
- TOMASI, T. E. (1979) Echolocation by the short-tailed shrew *Blarina brevicauda*. *J. Mammalogy* **60**, 751–759.
- VOGEL, P. (1969): Beobachtungen zum interspezifischen Verhalten der Hausspitzmaus (*Crocidura russula* Hermann, 1870). *Revue suisse Zool.* **76**, 1079–1086.
- (1978): Metabolic levels and biological strategies in shrews. In: Comparative physiology: primitive mammals. Ed. by K. SCHMIDT-NIELSEN, L. BOLIS and C. R. TAYLOR. London: Cambridge Univ. Press. pp. 170–180.
- WILLAN, K. (1979): Design and field tests of a modified small mammal livetrap. *S. Afr. J. Zool.* **14**, 81–84.

Authors addresses: R. M. BAXTER, Department of Zoology, University of Fort Hare, Private Bag X 1314, Alice, 5700 E. Cape and D. IRWIN, P. O. Box 10 151, Scottsville 3209, Natal, South Africa.